

EVIDENCE FOR THE HYBRID ORIGIN OF *CERCIDIUM*
SONORAE (LEGUMINOSAE: CAESALPINIOIDEAE) OF
NORTHWESTERN MEXICO

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Cercidium sonorae Rose & Johnston, one of the five members of the genus occurring in the Sonoran Desert, is found only within the distributional overlap of *C. microphyllum* (Torr.) Rose & Johnston and *C. praecox* (Ruiz & Pavón) Harms (fig. 1). Trees of *C. sonorae* are less abundant than those of either *C. microphyllum* or *C. praecox*; when they do occur, however, one or the other, or both, of the other two taxa have been noted to be somewhere in the vicinity. This distributional pattern and the morphological intermediacy of *C. sonorae* between *C. microphyllum* and *C. praecox* led to the hypothesis of its hybrid origin. *Cercidium molle* Johnston, known only from the type collection (Johnston 3877, Agua Verde Bay, Baja California, México) is considered to fall within the variational range of *C. sonorae* (Carter, 1974).

Cercidium microphyllum is a tree up to 8 m tall, with ascending branches that lend it a broomlike aspect. *Cercidium praecox* is usually rounded or flat-topped, 3 to 4 m tall, the branches spreading. It has very few lateral branches as compared with the other two taxa (fig. 2). *Cercidium sonorae* is a spreading tree 4 to 8 m tall, usually with rather lax branches. A comparison of other characters of these taxa is given in Table 1. Consideration of *C. sonorae* as a hybrid is based upon distribution, morphological intermediacy and variability, ultraviolet absorption patterns in flowers, and low reproductive potential as assessed by pollen stainability and seed set.

Differences in branching habit between the three taxa were determined by noting the number and length of the branchlets in the terminal 25 cm of a branch (fig. 2). *Cercidium sonorae* is intermediate in number of branchlets, but the branchlets are longer than those of either putative parent; this may account for the more lax appearance of the branches in trees of this taxon. In leaflet length, *C. sonorae* bears close resemblance to *C. praecox*, whereas in petiole length (fig. 3), it is close to *C. microphyllum*.

Recently, it has been demonstrated that flowers on herbarium sheets, when exposed to ultraviolet light, indicate absorption and reflection of ultraviolet rays (Horovitz and Cohen, 1972; Eisner et al., 1973). In preliminary studies on the significance of ultraviolet light absorptive and reflective properties to the biology of certain plants, C. E. Jones found that flowers of *Cercidium floridum* and *C. microphyllum* present a different aspect in ultraviolet light than in visible light; subsequent

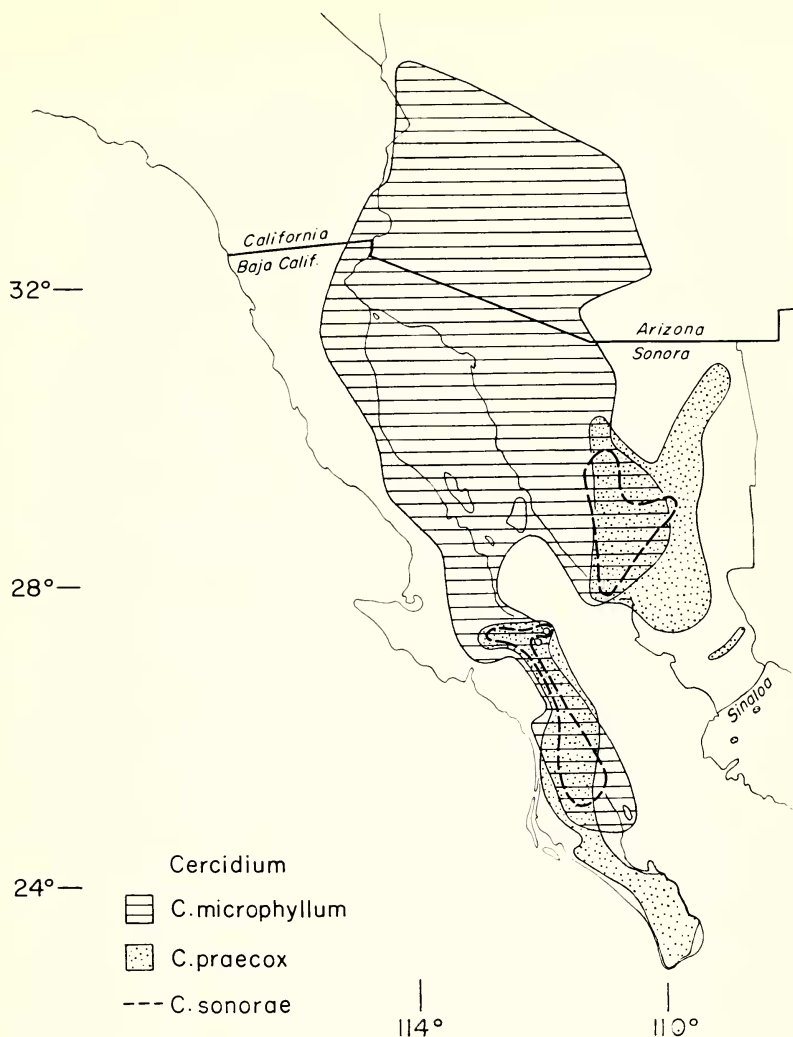


FIG. 1. Distribution of *Cercidium microphyllum*, *C. praecox*, and *C. sonorae* in the Sonoran Desert of northwestern Mexico and southwestern United States. Based on maps by Hastings, Turner, and Warren (1972).

observations indicated that pollinators were highly selective in visiting flowers having one or the other ultraviolet pattern (pers. comm., Jun 1972 and Sep 1973, Calif. State Univ. Fullerton). These observations were made along the lower Colorado River basin (California and Arizona), where the two species are sympatric and reach peak of bloom at approximately the same time and where only a few putative hybrids between these two taxa have been noted.

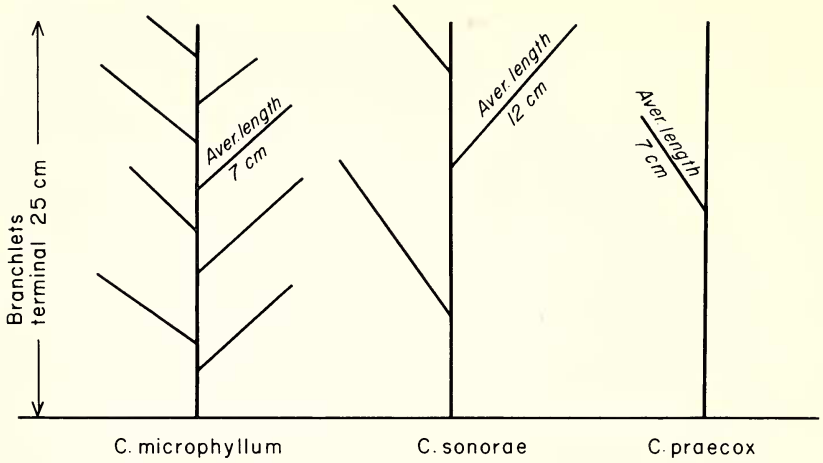


FIG. 2. Diagrammatic representation of the number of branchlets arising in the terminal 25 cm of branches of *Cercidium microphyllum*, *C. sonorae*, and *C. praecox*.

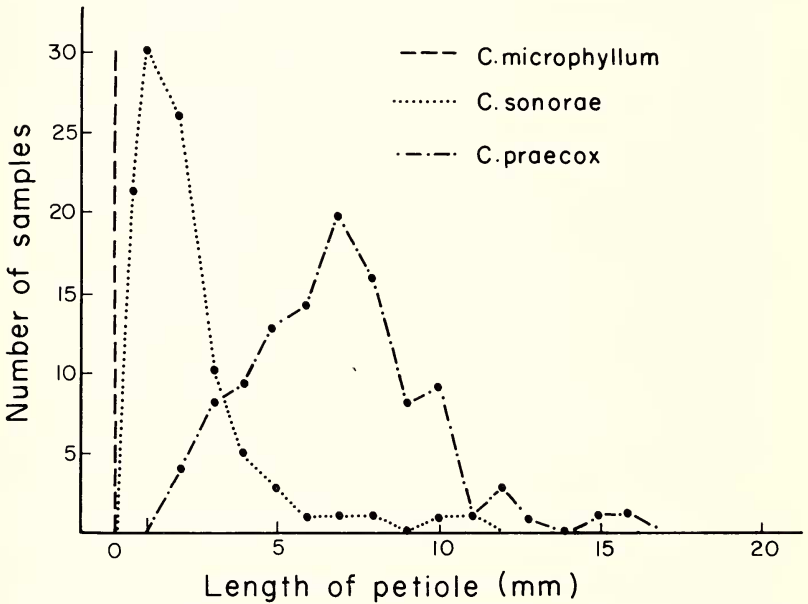


FIG. 3. Comparison of petiole lengths in *Cercidium microphyllum*, *C. sonorae*, and *C. praecox*.

Herbarium specimens of *Cercidium microphyllum*, *C. praecox*, and *C. sonorae* were examined under long-wave ultraviolet light to determine if the ultraviolet absorptive and reflective properties support the hypothesis of *C. sonorae* being of hybrid origin. All specimens examined

TABLE 1. COMPARATIVE CHART INDICATING THE INTERMEDIATE POSITION OF CERCIDIUM SONORAE BETWEEN ITS PUTATIVE PARENTS

CHARACTER SPECIES	<i>Cercidium microphyllum</i> "dipua" "dipuga"	<i>Cercidium sonoreae</i> "palo estribo"	<i>Cercidium praecox</i> "palo brea"
Branching pattern (terminal 25 cm.)	Many short branchlets, often stout.	A few slender branchlets.	An occasional stout branchlet.
Bark surface	Finely horizontally striate.	Smooth, or obscurely horizontally striate; sometimes with inconspicuous waxy coating.	Quadrate pustulate and waxy-coated.
color	Yellow-green, lower trunk gray.	Green to yellow-green, lower trunk gray.	Bright green throughout.
Axillary bud scales	Present, but usually not conspicuous.	From inconspicuous to conspicuous.	Abundant, dark, and conspicuous.
Axillary thorns	Lacking, the branchlets spine-tipped.	Present or lacking, slender.	Present, long and stout.
Inflorescence	Open racemes on terminal and sub-terminal branches.	Open racemes on terminal and sub-terminal branches.	Forming sub-sessile appearing clusters along old branches.
Flowers	Clawed upper petal white or creamy-white; other four petals yellow, the limb lanceolate or rhomboidal.	Clawed upper petal varying from creamy to yellow and with or without orange dots; other four petals ovate with pointed apex.	Petals all deep yellow, the upper clawed petal often orange-dotted; limb of other petals broadly ovate.
Legumes	Torulose, strongly tapered apically and basally, longitudinally striate-veined, not papery.	Somewhat constricted between the seeds, conspicuously longitudinally striate-veined, not papery.	Flat and papery, net-veined, not or scarcely constricted between seeds.
Seeds	Sub-globose, brown.	Oblong, mottled.	Oblong, mottled.
Leaflets number of pairs per pinna	Mean: 6.11 pairs Range: 1-13 pairs	Mean: 6.4 pairs Range: 4-12 pairs	Mean: 6.5 pairs Range: 3-13 pairs
length (mm)	Mean: 2.0 Range: 0.5-5.0	Mean: 3.5 Range: 2 - 6	Mean: 5.9 Range: 3 - 8
petiole length (mm)	Sessile	Mean: 2.0 Range: 0-6 (-12)	Mean: 7.6 Range: 3-19
Pollen viability	89 to 99 percent	42 to 76 percent	95 to 96 percent

For each character, the heavy horizontal rule indicates the resemblance of *C. sonoreae* to the putative parents.

were collected by the author in southern Baja California and in Sonora between 1960 and 1973. Each collection number refers to material from a single tree.

In *Cercidium microphyllum* (nine collections examined), all of the petals absorb ultraviolet light, i.e., the petals appear dark (fig. 4, CEMI), even though the upper petal in this species is white or creamy white under visible light and the other four petals are yellow.

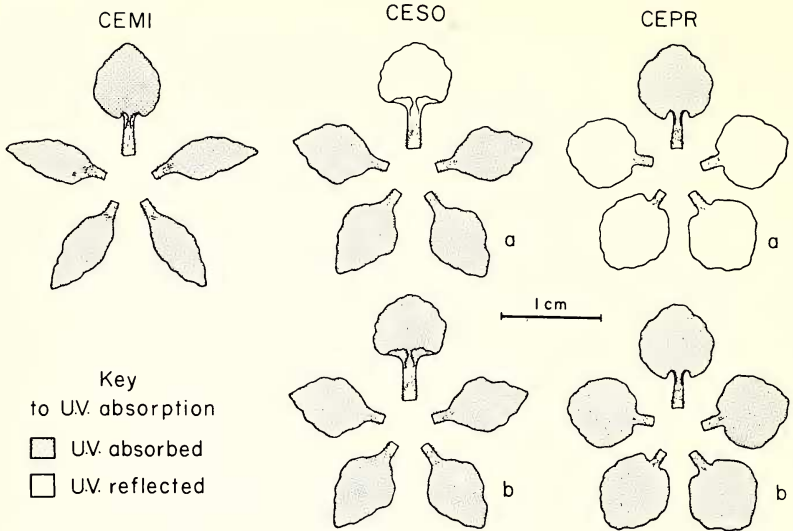


FIG. 4. Patterns of ultraviolet light absorption in flowers of *Cercidium microphyllum* (CEMI), *C. sonorae* (CESO), and *C. praecox* (CEPR). Degrees of ultraviolet light absorption (strong or weak) are not differentiated in the diagrams. Differences in petal shape between the three taxa (as noted in Table 1) are also portrayed in the figures. References to *a* and *b* are in text.

Petals of *C. praecox* are all a deep yellow under visible light. In all but two of the ten collections of *C. praecox* examined, the upper petal showed strong absorption of ultraviolet light, i.e., appeared very dark, and the other four petals reflected it, i.e., appeared yellow (fig. 4, CEPR a). In one of the two atypical collections (*Carter 4412*, between Rancho Segundo Paso and Misión San Javier, ca lat. 25°51' N, long. 111°32' W, Baja California Sur, 21 Apr 1962), five flowers exhibited weak absorption in all five petals (fig. 4, CEPR b). Two other flowers of the same collection showed weak absorption in the upper petal while the other four reflected ultraviolet light, i.e., these flowers approached the preponderant pattern for the taxon. In the other atypical collection of *C. praecox* (*Carter, Hastings & Turner 5597*, 20 km S of Carbo junction on highway between Hermosillo and Guaymas, Sonora, 3 May 1971), fifteen flowers were of the usual type for this species while one flower exhibited only a slight degree of absorption in the upper petal with the other four being reflective, and a second flower showed slight absorption in all five petals.

In *Cercidium sonorae* (14 collections examined), there are two main types of floral pattern under ultraviolet light, one with the upper petal reflective and the balance absorptive (fig. 4, CESO a), and the second with all the petals strongly absorptive (fig. 4, CESO b). In three of the fourteen collections examined both patterns were present in approxi-

mately equal numbers in each of the given trees (*Carter 5669* and *5671*, 55 km E of Villa Insurgentes on highway to Loreto, Baja California Sur, 3 May 1972; *Carter 5672*, base of hills NW of Loreto, Baja California Sur, 5 May 1972). Although Jones found that pollinators were highly selective in relation to different flower patterns in sympatric populations of *C. microphyllum* and *C. floridum*, it appears that such selectivity is not strongly operative in the case of *C. microphyllum*, *C. praecox*, and *C. sonorae*.

Differences in the absorption of ultraviolet light do not appear to be correlated with petal color. In *C. microphyllum* there is strong absorption of ultraviolet light in the upper white or creamy-white petal as well as in the balance of the petals, all of which are yellow. In *C. praecox*, wherein all five petals are deep yellow, the upper petal strongly absorbs and the others reflect ultraviolet light in the majority of cases. In *C. sonorae*, wherein the upper petal varies from nearly white through creamy yellow to yellow (and sometimes even splotched white and yellow), there appears to be no correlation of ultraviolet light absorption with these colors. However, greater stability of the ultraviolet pattern in the putative parents and variability of the pattern in *C. sonorae* lend support to the hypothesis of the hybrid origin of *C. sonorae*.

Unfortunately, ordinary herbarium specimens of *Cercidium* do not lend themselves to statistical studies of ultraviolet light absorption because in each specimen only a few flowers become pressed in such a position that all five petals are clearly displayed. In order to make a definitive study, all of the open flowers in an inflorescence should be spread out and pressed individually and more than one inflorescence per tree should be so prepared. In addition, it should be noted which flowers are pre- and which are post-anthesis in order to determine whether or not the stage of floral development is correlated with the degree of absorption of ultraviolet light. Such an approach might shed some light on the factors determining the absorption and reflection of ultraviolet light in *Cercidium* flowers.

Pollen viability (as indicated by aniline-blue lactophenol staining) is from 89 to 99 percent for *Cercidium microphyllum* and *C. praecox*, but only 42 to 76 percent for *C. sonorae* (Carter and Rem, 1974). Furthermore, field observations have shown that there is often poor seed-set on trees of *C. sonorae*, whereas trees of other species of *Cercidium* in the area evidence good seed-set [pers. comm. Hastings (ARIZ) to Carter, 24 May 1972]. The relatively lower fertility of *C. sonorae* gives strong support to the hypothesis of its hybrid origin.

Study of meiotic chromosomes of *Cercidium sonorae* might further substantiate the hypothesis of a hybrid origin. Unfortunately, the chromosomes of this taxon have yet to be studied. The single report in the literature for *C. sonorae* (Turner and Fearing, 1960) probably is based on misidentified material of *C. praecox* [pers. comm., R. M. Turner

(U.S.G.S., Tucson, Ariz.) to Carter, 23 Jun and 18 Aug 1972]. No voucher was preserved [pers. comm., B. L. Turner (TEX) to Carter, 5 Jul 1972].

From comparison of the several characters as made in figures 2, 3, and 4 and those summarized in Table 1, it can be seen that *Cercidium sonorae* is extremely variable, some of the characters bearing a close resemblance to those of *C. microphyllum* and other characters being like those of *C. praecox*. In still other features, such as the color of the upper petal, the entire gamut of variation between the conditions in the two parents is displayed. The position of the heavy horizontal lines in Table 1 indicates my concept of the resemblance of *C. sonorae* to its putative parents.

In conclusion, I refer to the discussion of hybridization by Stebbins (1950) in which he indicates that interspecific hybridization among higher plants has been shown to be rather common in nature. Most of the examples given, however, are of herbaceous plants. He goes on to say that first and succeeding generations of offspring of most natural hybrids are very likely to represent backcross types rather than true F_2 segregates (ibid, p. 261). The variation in *C. sonorae* may well be interpreted in this light.

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